Chapter 1

General introduction

All ecological interactions take place in space. Finding scarce food items may require extensive spatial searches. Depletion of plankton by filter feeders in tidal waters may be felt by competitors over extensive distances. Yet, early approaches to understand the effects of ecological interactions on population dynamics commonly neglected the spatial context, such as in the classical treatment of ecological interactions by Lotka and Volterra back in the 1920s, where the only dimension was time (Lotka, 1932; Volterra, 1926). Most of ecological theory has since been based on the mean field assumption, which presumes that ecological interactions within a certain area can well be described as a function of the mean density of the involved organisms. In reality, however, ecological interactions often have an explicit spatial scale, which is both common and persistent across a range of ecosystems (Levin, 1992; Levin and Segel, 1985). In no field has this become more apparent than in the study of spatial self-organization, where scale-dependent interplay of different ecological processes creates patterns and other forms of spatial organization even in landscapes that have otherwise little underlying heterogeneity.

Since the first spatially-explicit ecological models were proposed by Hassell, Comins and May (1991, 1994) in the 1990s to describe pattern formation, the processes that underlie spatial self-organization have become an important source of theoretical speculation. Nowadays, spatial self-organization and the baffling variety of spatial mosaics and patterns that this process can create appeals to many ecologists. Theoretical and empirical ecologists have used various methods to unravel the emergent effects of spatially self-organized patterns on ecosystem functioning in a wide range
of ecosystems (Pringle et al., 2010; van de Koppel et al., 2005; Guichard et al., 2003; Kefi et al., 2007; Klausmeier, 1999; Rietkerk and Van de Koppel, 2008). Yet, many questions are still unanswered, and self-organization remains one of the most poorly understood topics in ecology (May, 1999; Sole and Bascompte, 2006). An imminent question is how spatial interactions and the resulting complexity affect natural systems, both in qualitative terms, i.e. by improving biodiversity, and in quantitative terms, i.e. improving carrying capacity.

![Figure 1.1: Examples of spatial patterns in nature. (A) Regular striped patterns on the coat of a zebra; (B) sand ripple patterns on a beach; (C) labyrinth-shaped patterns on a mussel bed; (D) Diatom-induced sediment patterns on an intertidal flat (images C and D courtesy of Johan van de Koppel).](image)

Self-organized spatial patterns are widely observed in nature, including animal coat markings, ripples and dunes in sand, vegetation distribution in semiarid regions, seagrass beds, coral reef morphology, and even patterns of animal aggregation (see Figure 1.1 for examples). The emergence of spatial patterning has invoked the interest of scientists from different realms of science. For instance, ecologists have studied the formation of spatial patterns in ecosystems, while behavioral biologists focused on collective
animal behaviour (Ioannou et al., 2012), such as joint movement of fish in fish schools (Couzin et al., 2002; Parrish and Edelstein-Keshet, 1999; Theraulaz et al., 2002; Hemelrijk and Hildenbrandt, 2013). To unravel powerful analogies between different systems, theoretical scientists tried to unravel the principles behind pattern formation using a range of statistical, mathematical (Cavagna et al., 2010, 2013), and computer simulation tools (Sherratt, 2013, 2012). These tools include differential equations, stochastic models, self-propelled particle models, and individual-based models (Sumpter, 2010; Vicsek et al., 1995).

Spatial patterns in ecosystems

In the past decade, a number of studies have emerged that pointed at spatial patterns observed in natural ecosystems, such as regularly patterned bush lands in semi-arid ecosystems (Klausmeier, 1999; von Hardenberg et al., 2001; Rietkerk et al., 2002), patterned boreal peat lands (Rietkerk et al., 2004; Eppinga et al., 2009), patterned savanna ecosystems (Scanlon et al., 2007; Pringle et al., 2010), ribbon forests in the rocky mountains (Bekker and Malanson, 2008; Bekker, 2009), patterned biofilms in intertidal mud-flats (van de Koppel et al., 2005; Weerman et al., 2010), in tidal freshwater marshes (van de Koppel and Crain, 2006), and in mussel beds (van de Koppel et al., 2008). These examples reveal that spatial patterns occur widely across a range of ecosystems. Patterns in the spatial distribution of individuals or species, as well as their change, are features that have in the past been linked to spatial differences in environmental conditions. Recent experimental and theoretical investigations, however, have shown that ecological interactions, even in the absence of environmental heterogeneity, may induce complex spatial patterns (Murray, 2002; Reichenbach et al., 2007; van de Koppel et al., 2008). These spatial patterns are therefore labeled as “self-organized”, meaning that they result from the interactions of the species that make up the ecosystem, rather than being imposed from external forcing from, for instance, the landscape. Interesting examples are found in the spiral waves in mycobacterial (Igoshin et al., 2004) and insect host-parasitoid systems (Hassell et al., 1991, 1994), striped and labyrinth-shaped patterns in mussel beds (van de Koppel et al., 2008), and fractal-like patterns in competing strains of E. coli (Kerr et al., 2002).
What mechanisms drive pattern emergence?

One of the frontiers of ecological theory is to understand the mechanisms and implications of spatial self-organization in ecosystems (Eppinga et al., 2009; Rietkerk et al., 2004; Rietkerk and Van de Koppel, 2008). The diversity of possible ecological mechanisms that could drive pattern formations is bewildering, and a number of different models have arisen in the past decades to study their underlying principles (Eppinga et al., 2009; Eppinga, 2009). Here, I will quickly summarize the most important ones.

Turing’s activator-inhibitor principle

Regular spatial patterns are the most prominent form of spatial self-organization in ecology (Klausmeier, 1999; Rietkerk et al., 2002; Eppinga, 2009; Weerman, 2011; Hassell et al., 1991). Despite of them occurring in a wide variety of ecosystems, there are striking similarities in the morphology of the patterns across ecosystems, in the form of regular dotted, spotted, or banded patterns. Theoretical studies suggest that this similarity may originate from a common underlying principle, which was formulated mathematically as the activator-inhibitor principle by Alan Turing in 1952 (Turing, 1952). According to the activator-inhibitor principle, small-scale activation processes interact with large-scale inhibition to generate symmetry-breaking instability, leading to regular spatial patterns. This activator-inhibitor principle, in an ecological context called a scale-dependent feedback, has successful been applied in many ecosystems (Eppinga et al., 2009; van de Koppel and Crain, 2006; van de Koppel et al., 2005; Weerman et al., 2010; van der Heide et al., 2010a). Often, but not essentially, it involves a close interaction between organisms and their environment, where organisms locally modify their environment to improve overall growth conditions, but deplete an essential resource to inhibit population growth at larger spatial scales. This type of interaction cuts across many ecosystems to explain pattern formation and its effects on ecosystem functioning (see Rietkerk and Van de Koppel (2008) for an in-depth review). The experimental data has demonstrated that scale-dependent feedback between organisms and their environment gives a general explanation for regular pattern formation for many ecosystems (see Box I).
**Box I:** Experimental evidence of scale-dependent feedback in ecosystems

Even though the appearance of Turing patterns often seems obvious for many ecosystems, it is difficult to be sure they were produced by Turing's activator-inhibitor mechanism (also called a scale-dependent feedback), rather than some other mechanism.

In ecosystems, scale-dependent feedbacks emerge mainly from short-range facilitation through modification of the environment and long-range competition for resources. This short-distance positive feedback and long-distance negative feedback, irrespective of the precise mechanisms involved, can create regular spatial patterns.

There are only two direct experiments that support the existence of scale-dependent feedback mechanism in ecology. One of them was done by Van de Koppel and Crain (2006) on spatial patterns in the distribution of *Carex stricta* tussock. The results revealed a clear combination of positive and negative feedback on the tussocks growth, at a distance of 15 and 75 cm from the tussock center, respectively (see Figure 1). Another experiment was done by Bregje et al. (2008) on *Spartina anglica*, revealing a similar scale-dependent growth rate.

![Figure 1](image)

**Figure 1:** Experimental evidence of scale-dependent feedback. *Carex stricta* was transplanted at varying distance from tussock centers with and without aboveground standing crop. From Van de Koppel and Crain (2006).
Figure 1.2: Self-Organized patterns as indicator for catastrophic shifts in ecosystems. The bifurcation graph describes changes in equilibrium vegetation biomass as a function of environmental stress level. The insets maps of patterned vegetation: the dark colour represents vegetation and the light colour represents bare soil. From Rietkerk et al. (2004).

Why are self-organized spatial patterns important in ecology?

Theoretical models highlight that self-organized spatial patterns may have a wide variety of effects on the functioning of ecosystems (Kefi et al., 2007; Rietkerk et al., 2004) and ecosystem services (Pringle et al., 2010; van de Koppel et al., 2005; Gilad et al., 2004), in the form of increased productivity and ecological resilience. Self-organized ecosystems can foster high biodiversity and productivity, and improve the ability to withstand disturbance from external factors, typically referred to as resilience and robustness. This implies that self-organized ecosystems can continue to work when perturbed or when affected by adverse external factors or the failure of internal components (see Figure 1.2). For certain circumstances, the ecosystem may reconfigure when required, degrading in performance gradually rather than exhibiting a catastrophic transition. Finally, spatial
patterns can be used as indicator for imminent catastrophic shifts in ecosystems (Figure 1.2), highlighting the potential application of self-organization theory for ecological management and conservation (Rietkerk et al., 2004; Scheffer et al., 2009; Dakos et al., 2011; Kefi et al., 2007).

Despite of a wealth of possible applications, it remains a big challenge to simply explain observed spatial patterns in terms of the underlying mechanisms and the ecological processes on which these are based. Ecologists typically present self-organization theory as a putative explanation for spatial patterns observed in nature, but little evidence is generally presented that unravels the causality of pattern formation. Only rarely are alternative hypotheses about the mechanisms underlying observed patterns tested, or even compared (but see Eppinga (2009) and van de Koppel and Crain (2006)). Moreover, whether these alternate mechanisms affect the emergent properties of spatial self-organization for the functioning of ecosystems remains mostly unknown.

Mussel beds: a self-organized ecosystem

Large aggregations of mussels, generally called mussel beds, are a common feature of intertidal flats and subtidal areas in the Wadden Sea. Mussel beds can be between 1 to 10 ha in size (see Figure 1.3). Mussels are an important component of intertidal ecosystems and a major resource for aquaculture (van Leeuwen et al., 2010; van Leeuwen, 2008). Mussels consume the algae by filtering them from the overlying water layer, which is carried up onto the mussel bed by the tidal water flow. Because algae in the lower boundary layer are quickly depleted by mussels, mussels can affect algal concentrations over extensive spatial scales. On short timescales, exchange of water with higher water layers may replenish algal concentration in the benthic boundary later, but ultimately the main source of algae comes by far from the incoming tidal water (van de Koppel et al., 2005).

Large-scale patterns in mussel beds

Beds of young blue mussels in the Wadden Sea are typically characterized by banded patterns that are aligned perpendicular to the average incoming
tidal flow, and have a wavelength of approximately 6-10 meters. Within these bands, mussels can reach high densities of over 30 kg per square meter fresh weight (about 500 g dry biomass), alternating with almost bare sediment in the inter-band areas (van Leeuwen, 2008; van Leeuwen et al., 2010; Snover and Commito, 1998). These strikingly regular spatial patterns are found on homogenous tidal flats, which led to the hypothesis that they result from self-organization processes, caused by the interactions between facilitation at local scales and competition between individual mussels for algae at large scales (van de Koppel et al., 2005).

Van de Koppel et al. (2005) provided a potential explanation for the emergence of large-scale banded patterns, based on scale-dependent feedback processes. The model assumes that facilitation between mussels,
resulting from reduced losses due to predation and wave dislodgement within dense aggregations, as mussels bind to each other using byssus threads to form strong clusters and mats. Dense aggregations of mussels, however, will cause a strong competition for the limited availability of algal food, the effect of which may carry over extensive distances due to tidal flow. Therefore, algae act as a long-range inhibitor to limit mussel growth.

The blue mussel is an ecosystem engineer, in that it can exert substantial effects on its physical surroundings (van Leeuwen et al., 2010; van Leeuwen, 2008). Mussels modify their own habitat by accumulating large amount of sediment underneath the mussel mat. This way, mussel beds will influence total density and the distribution of fine sediments at both small and large scale (Hunt and Scheibling, 2001; Hunt et al., 2003). This can influence the foraging efficiency of the mussels, as the increased elevation, resulting from sediment accumulation, improves access for the mussels to the algal food in higher water layers. However, feedback that results from sediment accumulation on mussel bed pattern formation still has not been studied, neither theoretically, nor experimentally.

In this thesis, with regard to the feedback between sediment accumulation and mussel bed development, I address the following research question:

**RQ 1:** Can feedback between sediment accumulation and mussel growth provide an alternative mechanistic explanation for pattern formation in mussel beds? Also, how does it affect ecosystem functioning?

### Small-scale patterns in mussel beds

In the past years, a new type of spatial self-organization has been discovered in mussels beds that results from behavioral, rather then demographic processes. Here, mussels actively aggregate to form string and net-shaped clumps (Figure 1.4A). Experiments showed that this form of pattern formation is completely driven by active movement by the mussels (van de Koppel et al., 2008). Pattern development at this small scale is strikingly fast, where mussels aggregate into patterns from homogeneous starting conditions within hours.

This kind of small-scale patterns in mussel beds, which I call *behavioral*
self-organization, is remarkably different from Turing’s activator-inhibitor principle. According to the activator-inhibitor principle, spatial differentiation of growth conditions, caused by scale-dependent interactions between organisms, is a prerequisite for pattern formation to occur. Moreover, this activator-inhibitor principle requires at least two species to interact. Pattern formation in mussels occurs in just a single species. Second, the self-organization process results from animal movement rather than from growth and mortality processes.

Figure 1.4: Two ecosystems with patterning at multiple spatial scale. (A) Aerial images of mussel beds at different spatial scales, rope-shaped aggregation at less 1 m scale (left), banded patterns at 1-10 m scale (middle), concentrated beds at more than 100 m scale (right), pictures by Johan van de Koppel (left), Norbet Dankers (middle and right). (B) Image of seagrass bed in Shark Bay, with patterns at multiple spatial scales, picture from Google Earth.

Physical theory provides a suitable explanation for autonomous self-organization caused by movement processes, when explaining the phe-
nomenon of *phase separation*. Phase separation occurs where a single or two homogenously distributed chemical or physical species are separated into two spatial regions because of a dependence between movement velocity and local density. This mechanism was originally proposed by Cahn and Hilliard in the 1950s (Cahn and Hilliard, 1958). Recent experiments with mussels revealed that an essential element of aggregative pattern formation in mussel beds is that, similarly, movement is density dependent, where speed is negatively related to local mussel density (van de Koppel et al., 2008). Hitherto, the phase separation principle has mostly been applied in other, non-ecological disciplines, such as multiphase fluid flow, mineral exsolution and growth, and biological applications (Cohen and Murray, 1981; Bray, 2002; Cates et al., 2010). So far, no theory exists that provides a general explanation for movement-based self-organization in ecological systems. This points at a possibly very new principle of ecological self-organization, and possibly a new, ecological application for the, so-far, physical principle of phase separation.

Hence, in this thesis, I will address the research question:

**RQ 2:** Can behavioral, movement-based self-organization, as found in mussels but also in other ecosystems, be interpreted as a new ecological form of phase separation?

**Multiple-scale patterns in mussel beds, do they matter?**

A prevalent characteristic of life is its complexity at many levels of organization (Camazine et al., 2003; Parrish and Edelstein-Keshet, 1999). Self-organization is found in many biological processes (Meinhardt et al., 2003), ranging from early morphogenesis to ecosystem formation. Processes underlying spatial-self-organization can be molecular, enzymatic, behavioral, or demographic in nature. Theoretical studies of spatial self-organization in ecosystems, however, have for the mostly focused on single mechanisms when explaining pattern formation. Whether and how different mechanisms of spatial self-organization interact to shape complexity in ecosystems, remains largely unstudied.

As already mentioned above, an extensive body of literature has focused on the causes and implications of regular patterns formation in ecosystems. However, current understanding limits itself to regular spatial patterns
occurring at a single, fixed spatial scale. A number of observations suggests that spatial patterns can well occur at multiple scales within communities, one nested within the other. An example of this can be found in mussel beds (see Figure 1.4). For nested patterns in mussel beds, the small-scale patterns develop at scales of approximately 10 cm, while the other occur at large spatial scales of approximately 5-10 meters. Mussel beds are not a unique example of the occurrence of nested patterns. A similar nested pattern can be found in seagrass beds found in Shark bay (see Figure 1.4). As far as we know, self-organized, multiple-scale spatial patterns have not previously been investigated in ecology. Therefore, I ask the follow research question.

**RQ 3:** What ecological mechanisms drive the spatial patterns that appear at multiple spatial scale in mussel beds? How do they affect the functioning of mussel bed ecosystems?

**Does spatial heterogeneity affect the emergent properties of self-organized spatial patterns?**

As mentioned above, theoretical models highlight that self-organized spatial patterns can have important emergent effects on the functioning of ecosystems, for instance by increasing productivity, affecting the vulnerability to catastrophic shifts, and enhancing ecosystem persistence. However, most theoretical studies presume idealized, homogeneous environmental conditions, for instance by assuming a flat underlying landscape and an even influx of limiting resources. Field observations reveal that conspicuous large-scale gradients can occur, most likely resulting from changed environmental conditions, as found for instance in semiarid vegetation, or in mussel beds (see Figure 1.5). How does this spatial heterogeneity affect the emergent properties of the patterns? This question still is not clarified, neither in theoretical nor in experimental studies.

Mussel beds growing on intertidal mudflats are typically revealing strong heterogeneity in the properties of the spatial patterns, where thick bands are found at the sea side, while thinner bands are found as one moves onto the tidal flat. A possible explanation for this is that they are affected by large-scale food availability to the mussels. Models that apply homogeneous settings predict that beds are more productivity when
they are patterned, but also more vulnerable to regime shifts at low algal availability or high wave disturbance rates. However, whether these predictions still hold when large-scale gradients in environmental conditions are imposed in the model, remains unknown. Hence, using self-organized mussel beds as a case study, we address the following question.

**RQ 4:** What are the effects of self-induced gradients in food availability, generated by depletion of algae in higher water layers by the mussels, on the functioning
of self-organized mussel beds?

To answer this question, we assume that algae enter the system with the tidal water flow from the seaward boundary, and model their gradual depletion using a multilayer description of the water column. The theoretical predictions are compared with observations from real mussel beds.

Outline of the thesis

In this thesis, I will examine which are the dominant processes that explain pattern formation in mussel beds. Moreover, I will study how these processes affect ecosystem functioning, in term of productivity, resilience, and whether the patterns can be used as indicator for imminent collapse of mussel beds. My studies include field data, laboratory experiments, and mathematical models. Although these studies are based on a specific ecosystem —mussel beds—the conclusions have abroad implication that, in principle, should apply to different ecosystems.

In Chapter 1, I give an overview of the theory of spatial self-organization, where I will explain the questions that I have studied, and why they are current and important.

In Chapter 2, I pose alternative mechanisms to explain self-organization in mussel beds, based on field surveys of the relationship between sediment accumulation and mussel growth and density. By comparing a newly proposed mechanism with previous mechanisms explaining mussel bed patterning, we study whether the emergent properties, in term of ecological resilience, and productivity, are strongly dependent on the mechanistic explanation of pattern formation.

In Chapter 3, based on recent experiment results, I have reanalyzed the process of aggregative pattern formation of mussels. Here, we reveal a new class of self-organization mechanism, which is different from the well-known activator-inhibitor principle as developed by Turing. We prove mathematically that this new mechanism is similar to the physical principle of phase separation.

In Chapter 4, I study the origin and consequences of the nested
spatial patterns that many mussel beds exhibit. To understand underling mechanisms and the implications for ecosystem functioning of this complex nested patterning, I have developed an individual-based mathematical model. This model highlights how behavioral and demographic processes of pattern formation interact to determine the productivity and resilience of mussel beds.

In Chapter 5, using self-organized mussel beds as a case study, we study the implications of spatial heterogeneity for the functioning of self-organized ecosystems. The results, both mathematical and empirical, suggest that the physical context in which mussel beds exist (tidal water influx from the side of the bed containing the algae) generates strong, self-induced spatial heterogeneity in the patterning observed in mussel beds. Using our model analysis, we study how spatial heterogeneity in pattern properties affects the productivity and vulnerability of mussel bed ecosystems.

In Chapter 6, we compare the results that we obtained in chapter 3 with other studies in the literature. Current concepts of self-organized spatial patterns are mostly based on demographic processes involving organism growth, birth and mortality processes. In this chapter, I review a wide range of studies that point at density-dependent movement when explaining self-organized pattern formation, with examples from bacterial biofilms, ant behavior, and social insects. Our review highlights that density-dependent movement leads to self-organized patterns in many ecosystems, highlighting a new, previously ignored principle of spatial self-organization for ecological systems.

In Chapter 7, I will give a brief summary of my thesis, and provide a perspective on future questions about spatial self-organization that arise from the results presented in this thesis.